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An extraordinary new species of *Psyllipsocus* (Psocodea: 'Psocoptera': Psyllipsocidae) from the Biosphere Reserve Sierra de Huautla, Morelos, Mexico

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Abstract: The insect species *Psyllipsocus stupendus* spec. nov., living on rock outcrops, is described and illustrated from central Mexico (Morelos state). Although the general morphology is typical for a *Psyllipsocus* species, both male and female are characterized by very peculiar genitalia. In the male, the phallosome has a pair of long pointed claspers and, surprisingly, the basal struts are not anteriorly but posteriorly directed. In the female, the first and second ovipositor valvulae, usually much reduced in this genus, are well developed and strongly sclerotized, forming a tube-like structure together with the sclerotized wall of the proximal part of the vagina. The dorsal wall of the female genital chamber is transversally double-folded, resulting in a ventral main compartment and an eversible dorsal compartment. The opening of the spermathecal duct (spermapore) opens proximally into the dorsal compartment. A similar structure of the female genital chamber has never been observed in Psocoptera before. Some functional hypotheses are discussed and it is postulated that a special form of selective pressure, probably due to sexual selection, might have favoured the evolution of these unique genital structures.

Keywords: Insecta - female genital chamber - sclerotized vagina - phallic claspers.

INTRODUCTION

The New World Psyllipsocidae ('Psocoptera': Trogiomorpha) are relatively well studied and comprehensive keys to genera and species are available (Mockford, 1993, 2011; Lienhard & Ferreira, 2015). At present, the genus *Psyllipsocus* Selys-Longchamps, 1872, includes 40 New World species, 24 of them known from North and Middle America (Mockford, 2011) and 18 from South America (Lienhard & Ferreira, 2015).

Many species of this genus live on bark of trees, in soil litter or on lichen-covered rock outcrops (Mockford, 2011), while many others are known only from caves (Lienhard & Ferreira, 2015); one of them, *Psyllipsocus ramburii* Selys-Longchamps, 1872, is a cosmopolitan domestic species (Lienhard & Smithers, 2002). Here we describe a new Mexican species living on rock outcrops in the mountains of the Sierra de Huautla (Morelos state). Its general morphology is typical for the genus *Psyllipsocus* but it is characterized by very peculiar male and female genitalia.

MATERIAL AND METHODS

The material examined is deposited in the following institutions: Muséum d'histoire naturelle, Geneva, Switzerland (MHNG); National Insect Collection at Instituto de Biología, Universidad Nacional Autónoma de México (CNIN).

Dissection and slide-mounting followed the methods described by Lienhard (1998). The pilosity of wing veins is heavily damaged in the material studied. For Fig. 1A it was reconstructed on the basis of the insertion points of the hairs, which are readily visible in slide-mounted wings, and of the few hairs which were not lost. The length of these hairs was considered as representative for the pilosity of the entire wing, based on the observation that in *Psyllipsocus* the length of wing ciliation is normally uniform over the whole wing. In the description, the terms microspades organ (pedicel), coxal organ (hindleg), setal organ (paraproct), phallic cradle and endophallic tube (male genitalia) are used *sensu* Mockford (1993, 2011).

Abbreviations used in the description: AP = areola postica (a marginal cell in forewing formed by veins CuA1 and CuA2); bcc = length of basal closed cell in forewing; BL

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= body length (in alcohol); dcc = length of distal closed eell in forewing; F = hindfemur (length); FW = forewing (length); FWw = forewing (greatest width); HW = hindwing (length); IO/D = shortest distance between compound eyes divided by longitudinal diameter of compound eye in dorsal view of head; P2 = second article of maxillary palp; P4 = fourth (terminal) article of maxillary palp; T = hindtibia (length); t1, t2, t3 = tarsomeres of hindtarsus (length, measured from condyle to condyle); v1, v2, v3 = first (ventral), second (dorsal) and third (external) ovipositor valvula respectively. Abbreviations of wing veins are used according to Yoshizawa (2005). For other abbreviations see legends to the figures.

TAXONOMIC PART

Psyllipsocus stupendus sp. nov.

Figs 1-4

Holotype: MHNG; male (slide-mounted); Mexieo, Morelos state, Biosphere Reserve Sierra de Huautla, 2.5 km N and 4 km W of the Centro de Educación Ambiental e Investigación Sierra de Huautla (CEAMISH), 940 m; 12.-17.iii.1996, Malaise trap 2; 18° 27'.671 N, 99° 02'.475 W [right wings and left maxillary palp lacking].

Paratypes: MHNG and CNIN (slide-mounted or in alcohol). – 6 males, 6 females (one of them allotype); same locality as for holotype; ii.-vi.1996, Malaise traps. – 1 female, 1 nymph; same loeality, on rock outcrop; 9.vi.1996, leg. T. Martínez. – 1 female; Mexico, Morelos state, Biosphere Reserve Sierra de Huautla, Municipio de Tepalcingo, El Limón de Cuauchichinola, 1200 m, on rock outcrop; 11.v.1996, leg T. Martínez.

Diagnosis: This new species can be distinguished from all known species of the genus *Psyllipsocus* by the very particular male and female genitalia, the general structure of which is already observable in non-dissected specimens in alcohol.

Etymology: The species epithet (Latin: stupendus, -a, -um) refers to the astonishing male and female genitalic structures.

Description: General colouration yellowish to medium brown. Head without particular facial markings, eompound eye brown, maxillary palp uniformly light to medium brown, antenna light brown. Legs: femur light brown, tibia medium brown with whitish sub-basal zone, tarsus medium brown. Forewing hyaline with more or less intense brown markings along several veins in apical half (Fig. 1A), hindwing hyaline (Fig. 1B). Abdomen whitish, basally and laterally with some brown hypodermal pigment, terminalia brown.

Both sexes macropterous (Fig. 1AB). Forewing: Rs and M fused for a length; distal closed cell slightly shorter than marginal length of pterostigma and much shorter than basal closed cell (bcc/dcc ≈ 3.6); first portion of pterostigmal R1 about equal in length to R1-Rs crossvein; CuA1 strongly curved, AP relativly short and high. Hindwing: Basal portion of Rs not differentiated and R1 originating from Rs-M fusion, thus closed cell triangular. Three ocelli present. Pilosity of frons and vertex almost uniform. Antenna with at least 23 segments (most antennae damaged); antennal flagellomeres with uneven surface (due to insertion points of long and relatively thick setae), in basal half of antenna maximal length of flagellar hairs about 5x greatest width of their flagellomeres; pedicellar microspades organ weakly developed (with only one unit). P2 with a weakly differentiated stout sensillum in basal half (somewhat thicker than other setae of similar length); P4 slender hatchet-shaped, with a prominent subapical sensillum (Fig. 1F). Lacinial tip as in Fig. 1E. Pretarsal claws simple, symmetrical, with a small preapical denticle; hind legs with well-developed coxal organ. Epiproct and paraproct simple in both sexes (Fig. 1G), anal spine long, setal organ consisting of two fine setae of about equal length, but the ventral seta somewhat thicker than the dorsal one, paraproctal sensorium with 6-7 fine trichobothria on basal florets and one normal seta.

Male genitalia: Hypandrium and phallosome forming a ventrally bulged strueture of about half the length of the abdomen, laterally articulated to the sclerotized rod-like antero-lateral margin of the clunium (Fig. 1C). Hypandrium with a distinct posterior lobe (Fig. 1D); some long hairs on the lobe and near its base, remaining pilosity shorter (pilosity not shown in the figures); near base of the posterior lobe a pair of small dorsal hooked sclerites (Figs 1D, 2B), probably linked by ligaments to the phallic cradle and/or to the endophallic tube. Phallic cradle differentiated as a well-sclerotized frame on inner wall of hypandrium (Fig. 2A). Phallosome complex (Figs 1D, 2C), with a pair of slender, movable, slightly curved and acutely pointed claspers; endophallic tube basally on each side with a half-moon shaped plate and distally tapering towards a pair of narrowly rounded and slightly curved tips; a pair of posteriorly directed basal struts inserted medially near anterior margin of hypandrium (forming a posteriorly opened V in ventral view; see Fig. 1CD, interrupted lines), each strut linked to phallic cradle by a less sclerotized foliaceous strueture (Fig. 2C, dotted lines) attached on a small lateral denticle situated in about one third of its length.

Female genitalia: Complex sclerotized structures of v1, v2, vagina and spermapore plate readily visible through the largely membranous subgenital plate in ventral view (Fig. 1G). Subgenital plate membranous dorsally, at most weakly sclerotized ventrally, roughly triangular, bearing hairs of medium length on ventral surface but no particularly long setae on hind margin. Gonapophysis v3 typieal for the genus (Fig. 3A), almost rectangular, weakly sclerotized, bearing some stouter laterodistal

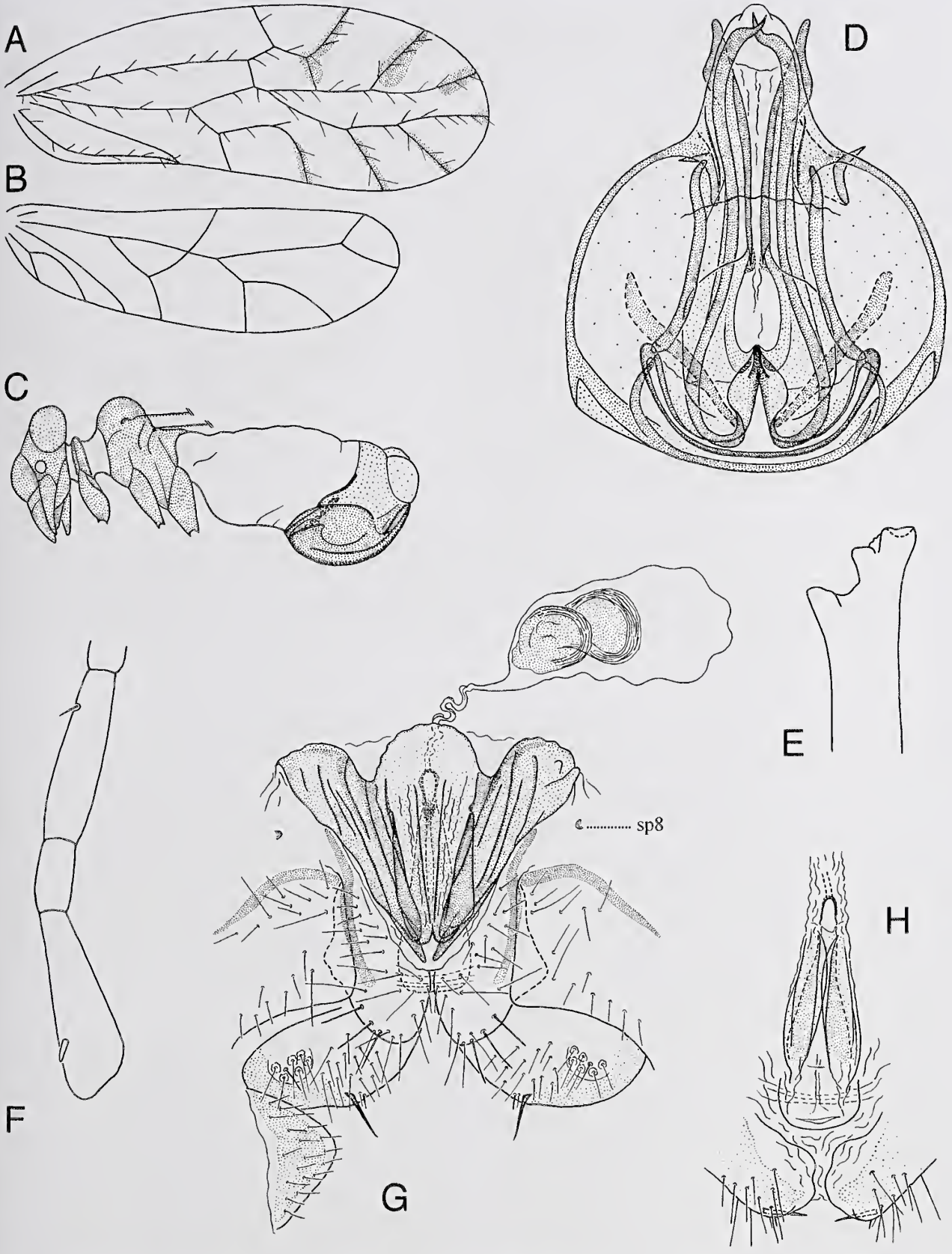

Fig. 1. *Psyllipsocus stupendus* sp. nov. (A) Forewing, female. (B) Hindwing, female. (C) Male habitus, lateral view (antennae, palps, legs and wings not shown). (D) Male holotype, hypandrium and phallosome, ventral view (pilosity not figured; basal struts shown by interrupted lines). (E) Lacinial tip, male. (F) Maxillary palp, male (ordinary pilosity not shown). (G) Female allotype (no. 8162), ventral view of dissected abdominal apex, see also Fig. 4B (pilosity of subgenital plate not shown; sp8 = spiracle of 8th segment). (H) Female paratype (no. 8163), spermapore plate and distal parts of paraprocts, ventral view, see also Fig. 4C.

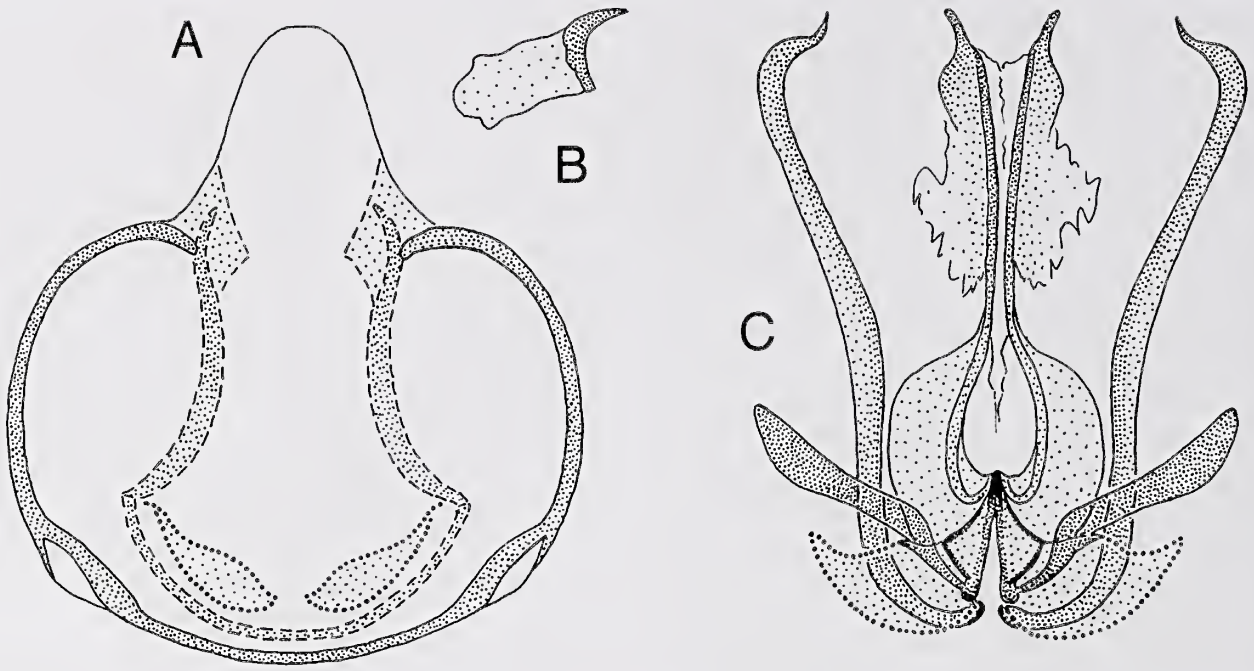

Fig. 2. *Psyllipsocus stupendus* sp. nov., schematic representation of male genitalia. (A) Hypandrium with phallic cradle (interrupted lines) and basal connecting sclerites (dotted lines) between phallic cradle and phallic sclerites (medially detached from phallic sclerites), ventral view. (B) Detached right hooked sclerite with part of ligament (in situ situated dorsally near base of posterior hypandrial lobe, see Fig. 1D). (C) Phallic claspers, endophallic tube, basal struts and basal connecting sclerites (dotted lines, laterally detached from phallic cradle), dorsal view; endophallic tube damaged laterally in posterior half by pulling out of phallic cradle during dissection.

setae (somewhat thicker than other setae of same length); v1 and v2 well-developed, elongated and strongly sclerotized (Fig. 3AB), basally widened and connected to the sclerotized and longitudinally folded dorsal wall of the vagina (Fig. 3B). Posterior part of this selerotized vaginal tube laterally articulated to its anterior part by a joint-like connection (x in Fig. 3B). Dorsal wall of the genital chamber transversally double-folded, resulting in a ventral main compartment, dorsally delimited by the sclerotized vaginal wall, and a dorsal secondary compartment, dorsally delimited by the spermapore plate (Fig. 4B). Spermapore plate elongated and well-sclerotized, with a longitudinal ventral bulge on each side covering a region of glandular tissue (Fig. 3B, interrupted lines); spermapore opened into an ovally semicircular sclerite at the anterior end of the spermapore plate (Figs 1H, 3B), situated proximally in the dorsal compartment of the genital chamber (Fig. 4B). Spermatheca thin-walled (Fig. 1G), very fragile, its duct greatly coiled; spermatophore only observed in one female (Fig. 1G: the structure figured may correspond to two simple spermatophores or to one more complex spermatophore).

Dimensions: *Male holotype*: BL = 1.7 mm; FW = 1820 µm; FWw = 650 µm; FW/FWw = 2.8; HW = 1510 µm; F = 342 µm; T = 720 µm; t1 = 270 µm; t2 = 45 µm; t3 = 54 µm; IO/D = 1.41. – *Female allotype*: BL = 1.8 mm; FW = 1750 µm; FWw = 650 µm; FW/FWw = 2.7; HW = 1440 µm; F = 348 µm; T = 715 µm; t1 = 260 µm; t2 = 47 µm; t3 = 51 µm; IO/D = 1.44.

Distribution: Mexico, Morelos state, mountains of the Sierra de Huautla Biosphere Reserve, on rock outcrops (but most known specimens collected in Malaise traps without indication of biotope or microhabitat).

Type locality: Mexico, Morelos state, Sierra de Huautla Biosphere Reserve, 2.5 km N and 4 km W of the Centro de Edueaeión Ambiental e Investigación Sierra de Huautla (CEAMISH), 940 m, 18° 27'.671 N, 99° 02'.475 W.

Remarks: The new species seems to be related to a group of North and Middle American speeies characterized by distally elongated phallic structures with proximal insertion of a V-shaped pair of basal struts. The following species listed by Mockford (2011) show this type of male genitalia: *P. albipalpus* Mockford, 2011 (Mexico), *P. apache* Mockford, 2011 (Southwestern USA), *P. flexuosus* Mockford, 2011 (Guatemala), *P. maculatus* Garcia Aldrete, 1993 (Mexico, USA), *P. oculatus* Gurney, 1943 (Mexico, USA), *P. poblanus* Mockford, 2011 (Mexico), *P. regiomontanus* Mockford, 2011 (Mexico), *P. squamatus* Mockford, 2011 (Mexico), *P. subterraneus* Mockford, 2011 (USA: Texas). In these speeies the arms of the basal struts are anteriorly directed, as in all other

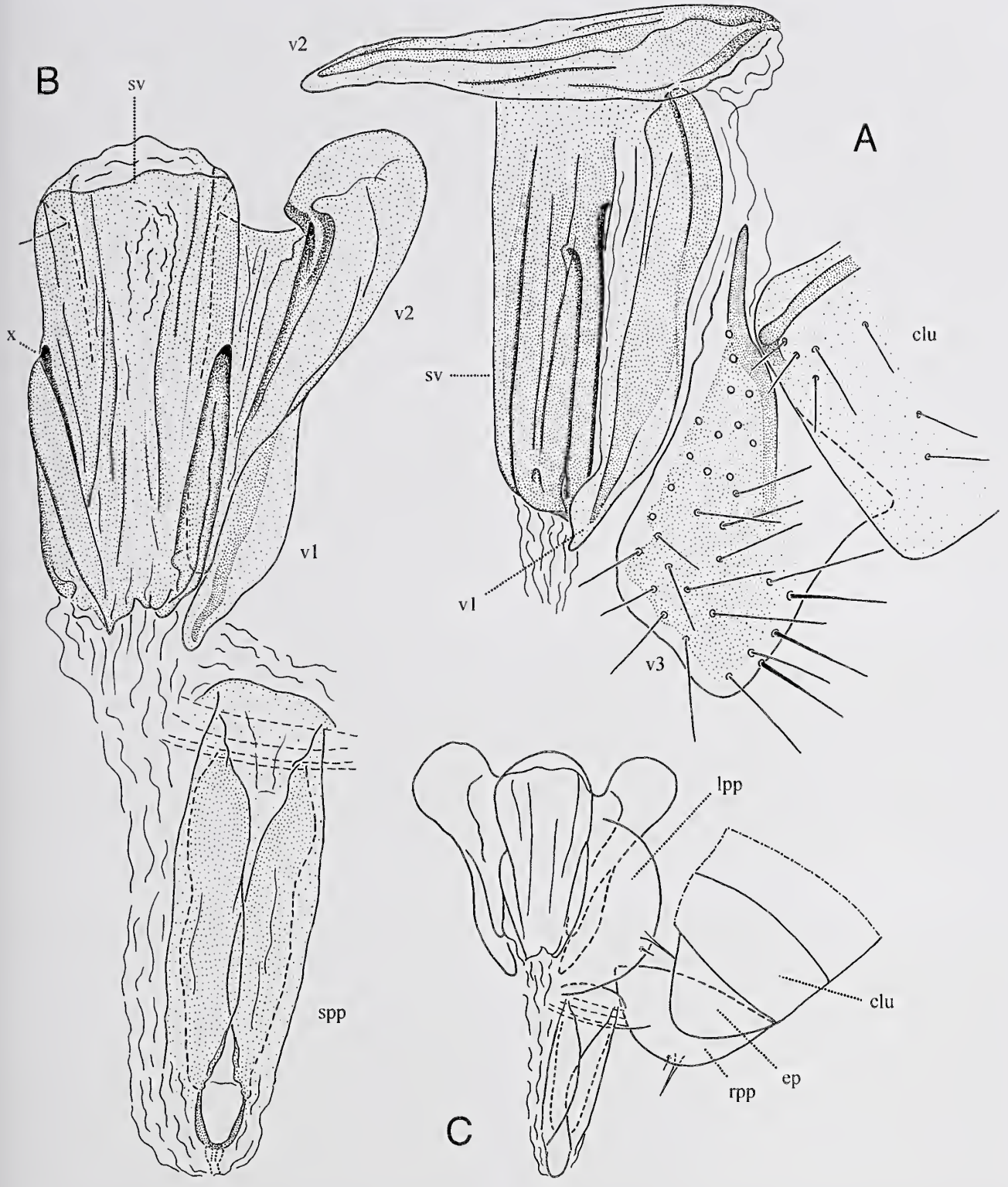

Fig. 3. *Psyllipsocus stupendus* sp. nov. (A) Female paratype (no. 8163), left latero-ventral part of clunium (ventral view), left ovipositor valvulae (v2 spread out) and sclerotized part of vagina (ventral to ventro-lateral view, somewhat deformed by slide mounting), see also Fig 4C. (B) Female paratype (no. 8164), right v1 and v2, sclerotized part of vagina and evaginated spermapore plate (dorsal view; i.e. direct view on ventral side of spermapore plate), see also Figs 3C and 4E. (C) Schematic representation of dissected abdominal apex of female no. 8164, see also Figs 3B and 4E. Abbreviations: clu = clunium; ep = epiproct; lpp = left paraproct; rpp = right paraproct; spp = spermapore plate; sv = sclerotized part of vagina; v1, v2, v3 = first (ventral), second (dorsal) and third (external) ovipositor valvula respectively; x = joint-like structure in sclerotized lateral vaginal wall.

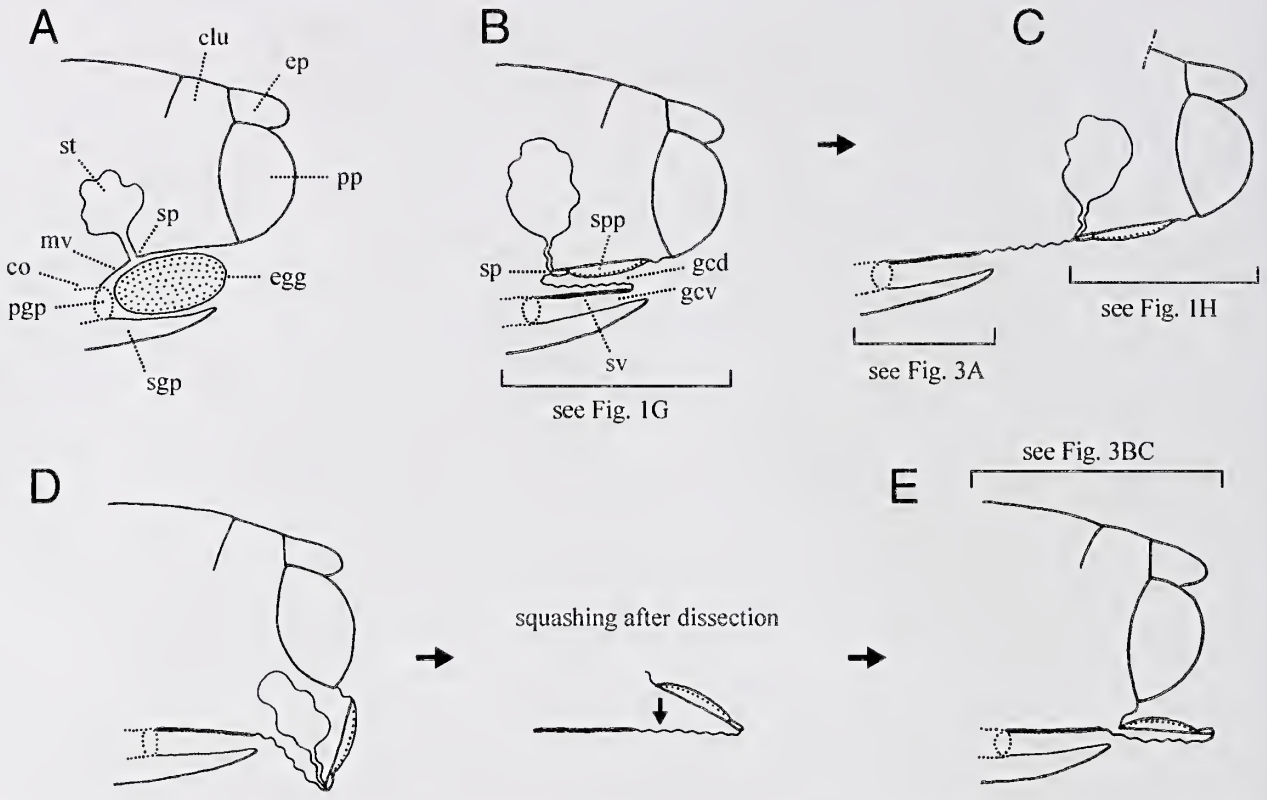

Fig. 4. Schematic representation of female abdominal apex, lateral view (ovipositor valvulae not shown). (A) General scheme of the abdominal apex of a typical female psocid, with egg in position for fertilization (modified after Weber, 1931 and Badonnel, 1951). (B-E) *Psyllipsocus stupendus* sp. nov., with indication of non-schematic figures showing further details. (B) Normal resting position (females no. 8162 and 8163), ventral side of spp marked with a dotted line (lumen of gcd much exaggerated). (C) Female no. 8163, after dissection. (D) Female no. 8164, with evaginated gcd (artifact? – see Discussion). (E) Same female after dissection. Abbreviations: clu = clunium; co = common oviduct; ep = epiproct; gcd = genital chamber, dorsal compartment; gcv = genital chamber, ventral compartment; mv = membranous vagina; pgp = primary gonopore (opening of common oviduct); pp = paraproct; sgp = subgenital plate; sp = spermapore (opening of spermathecal duct); spp = spermapore plate; st = spermatheca; sv = sclerotized part of vagina.

species of the genus that have well-developed basal struts. In *P. stupendus*, the structures which are here considered as homologous to the basal struts (see description) are posteriorly directed (forming a posteriorly opened V), probably due to the presence of extremely elongated phallic sclerites. The brachypterous species *P. kintpuashi* Mockford, 2011, the male of which is not known, may also be related to *P. stupendus*. Its female has some stouter laterodistal setae on v3 and the spermathecal duct is greatly coiled, similar to *P. stupendus*. A tendency to sclerotization of the vaginal wall has never previously been observed in the genus *Psyllipsocus*, and in all known species v2 and v3 are relatively short and membranous or only weakly sclerotized.

In spite of the striking autapomorphic genital characters of *P. stupendus* it is at present not justified to consider this species as a representative of a new genus. Concerning the non-genitalic structures, it fits well in the genus *Psyllipsocus*, and it is almost certain that this genus would become paraphyletic by a generic separation of *P. stupendus*. For further discussion see below.

DISCUSSION

In two of the three dissected females of *P. stupendus*, the genitalia were in normal resting position (see Figs 1G, 4B), as in the other alcohol-preserved females of the present material. That of the female no. 8164 show an evaginated dorsal compartment of the genital chamber (Fig. 4D), although this may be an artifact, possibly due to stress during fixation in alcohol. Without detailed observations of copulation and oviposition it is impossible to make a sound functional interpretation of the unusual genital morphology in *P. stupendus*. It may nontheless be of interest to present some preliminary hypotheses about the functional morphology of the complex male and female genitalic structures in this species.

Fig. 4A shows the standard structure of female terminalia in Psocoptera. In some psocids the vagina (genital

chamber) is subdivided by a membranous transversal fold of its dorsal wall in a ventral main compartment and a smaller dorsal compartment (e. g. *Stenopsocus*, see Badonnel, 1934). The spermathecal duct opens directly into the main compartment (Weber, 1931) or into the dorsal compartment near the distal part of the ventral compartment (Badonnel, 1934, 1951). For fertilization the sperm is released from the spermatheca and reaches the egg when it moves past the spermapore (Fig. 4A).

In the female of *P. stupendus* the dorsal wall of the genital chamber is transversally double-folded; the ventral compartment is dorsally delimited by the sclerotized part of the vagina; the dorsal compartment is ventrally delimited by a thin membrane and dorsally by the elongate spermapore plate which bears proximally the opening of the spermathecal duct (Fig. 4B). In the resting position, the distal end of the spermapore plate slightly surpasses the posterior end of the sclerotized vaginal wall (Figs 1G, 4B). The situation after dissection of the terminalia (Fig. 4C) and the observation of the evaginated dorsal compartment in the female no. 8164 (Fig. 4DE) show that the membranous ventral wall of the dorsal compartment is attached to the distal end of the sclerotized part of the vaginal wall and entirely separated from the sclerotized dorsal wall of the ventral compartment. Thus, the position of the spermapore plate may vary during copulation and oviposition depending on the extent of evagination of the eversible dorsal compartment.

Assuming that the egg passes through the ventral compartment while female genitalia are in resting position (Fig. 4B), it cannot enter in direct contact with the spermapore for fertilization. In this case, the sperm released from the spermatheca would have to swim toward the distal end of the spermapore plate before reaching the egg, probably passing between the lateral bulges of the spermapore plate which contain glandular tissue (Fig. 3B). Fertilization of the eggs seems therefore more complicated than in the standard situation, due to the presence of the sclerotized proximal part of the vaginal wall.

The presence of a pair of strongly sclerotized, apically curved and pointed phallic claspers (Fig. 2C), previously unknown in the genus *Psyllipsocus*, suggests that the sclerotized part of the vagina may have a protective function against traumatic effects of copulation, reminiscent of particular sclerotized structures associated with the vulvar area in Miridae (Heteroptera) which are interpreted as a defence system for the female against potential wounding by the male organ (Pluot-Sigwalt & Matocq, 2006). But the sclerotized part of the vagina may also provide new anchoring sites on which males can hold the mate by using their unique phallic claspers. Alternatively, it is also possible that the sclerotized vagina forms a tube-like functional unit together with the sclerotized first and second ovipositor valvulae. The presence of much reduced and weakly sclerotized v1 and v2 in all other species of *Psyllipsocus* suggests that these ovipositor valvulae may have a particular function in *P. stupendus*, possibly in combination with the adjacent sclerotized vaginal wall.

In the genus *Neotrogla* Lienhard, 2010, belonging to the related trogiomorphan family Prionoglarididae, structures associated with the spermapore are inserted deep into the male genital chamber during copulation (Yoshizawa *et al.*, 2014), which suggests the possibility of a somewhat similar mechanism in *P. stupendus*. The close contact between the female spermapore and the opening of the male seminal duct, indispensable for the transmission of the spermatophore in the suborder Trogiomorpha (Klier, 1956; Yoshizawa *et al.*, 2014) may be obtained in *P. stupendus* by evagination of the dorsal compartment of the female genital chamber and the shallow insertion of the spermapore plate into the male genitalia. During copulation the phallic claspers may drag the extendable part of the female genitalia into the male body. An example of female genitalia shallowly inserted into the male abdomen in this way is known in the cricket *Gryllus bimaculatus* De Geer, 1773; in this species the female copulatory papilla, bearing the opening of the spermathecal duct, is protruded and enters the male genital cavity where genital coupling is achieved (Sakai & Kumashiro, 2004).

Thus, the unique structures of male and female genitalia in *P. stupendus* may result from a reproductive biology which differs considerably from that of the other species of the genus. A special form of selective pressure based on sexual selection may be at the origin of the very particular genital structures in this species, while the natural (ecological) selection remains similar to most other species of *Psyllipsocus*, favouring the uniform general morphology (see the similar hypotheses for Zoraptera in Mashimo *et al.*, 2014).

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